

# Drip-tips do not impair the development of epiphyllous rain-forest lichen communities

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**Abstract:** Drip-tips are a common phenomenon in tropical rain forests, often believed to facilitate drainage of water from the leaf surface and, in that way, reduce epiphyll growth. Some authors suggest a function in reducing splash soil erosion, leaching of substances from the leaf, and light reflectance, while other studies did not find any such correlations. We used an experimental approach to test for the effect of drip-tips on the development of epiphyllous lichen communities. Artificial leaves with and without pronounced drip-tips were exposed in a tropical lowland rain forest at La Selva Biological Station (Costa Rica) for a period of 38 mo, and the physical behaviour of rainwater was tested. On leaves with drip-tips, the water ran off in small, frequent drops 8–30 mm<sup>3</sup> in size. On leaves without drip-tips, the water accumulated in the apex region and dripped off periodically in large drops 50–150 mm<sup>3</sup> in size. Nevertheless, there was no significant difference in the development of epiphyllous lichen communities on leaves with and without drip-tips, in terms of area covered, species richness and composition. However, leaves without drip-tips had more debris accumulated in the apex region and, at the same time, fewer lichen species present in this region. Thus, while drip-tips do have an influence on how water is channelled off the leaf surface, they do not impair the development of epiphyllous lichen communities, except for the apex region where the presence of drip-tips does in fact enhance, not reduce, the establishment of lichens, by preventing the accumulation of debris. We conclude that, while drip-tips may have an ecological function, this function is unrelated to the development of epiphyllous lichen communities.

**Key Words:** Costa Rica, drip-tips, lichen, rain forest

## INTRODUCTION

A striking feature of tropical rain forests is the abundance and diversity of epiphytism. Virtually all plant surfaces are colonized, and tiny plants, lichens and fungi even find their niche on the surface of living leaves (Lücking 1997, 2001a; Pócs 1978, Richards 1996). Indeed, ‘... nirgens offenbart sich die Lebenskraft der Tropen so eindringlich, wie in einem von Epiphyllen überwucherten und trotzdem noch immer lebensfähigen Trägerblatt... [... nowhere is the vitality of the tropics more apparent as in a leaf overgrown by epiphylls while still remaining functional...]’ (Vareschi 1980: 45). Another phenomenon is the abundance of leaves with prolonged, narrow apices, called drip-tips (Richards 1996, Vareschi 1980). These two phenomena have been connected ever since early researchers (Jungner

1891, Stahl 1893) postulated that drip-tips facilitate the drainage of water from the leaf surface, and thus reduce the growth of epiphylls, believed to negatively affect the photosynthetic performance of the leaf. Epiphyllous lichen and bryophyte thalli indeed absorb 30–70% of the light that would otherwise reach the leaf surface (Anthony *et al.* 2002, Coley *et al.* 1993, Lücking 2001a), although it has also been shown that leaves can acclimate to such conditions by increasing their chlorophyll concentration in the epiphyll-covered parts, thus behaving like ‘shade’ leaves (Anthony *et al.* 2002, Hawksworth 2003, Moore 2003). Yet, it seems evident that rain-forest plants growing under low-light conditions would have evolved defence mechanisms to prevent epiphyll growth, and the drip-tip has been the foremost candidate to represent such a mechanism.

Although this has been settled in many textbooks, few studies have addressed the effect of drip-tips on water drainage or epiphyll growth, and the results are ambiguous. While there is evidence that drip-tips facilitate

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the drainage of water (Dean & Smith 1978, Ivey & De Silva 2001, Jungner 1891, Lightbody 1985, Stahl 1893, Williamson 1981, Williamson *et al.* 1983) and are particularly common in seasonally wet lowland rain forests (Schneider *et al.* 2003, Vareschi 1980), other studies contradict these findings (Ellenberg 1985, Seybold 1957) and suggest that drip-tips represent functionless, ontogenetic residuals of budless leaves. The same applies to whether drip-tips reduce epiphyll growth: whereas evidence for this hypothesis is indicated by some authors (Dean & Smith 1978, Jungner 1891), other studies did not find such a correlation (Busse 1905, Fitting 1910, Ivey & De Silva 2001). Lücking (1998a) even suggested that drip-tips may enhance colonization by epiphylls, due to the particular nature of their diaspores. Many epiphylls, in particular early colonizers, produce diaspores that are dispersed by rain splash, but then require rapid drying of the leaf to be able to adhere to its surface (Degenkolbe 1937, Lücking 1997, 1998a; Sanders 2002).

Despite the abundant literature discussing the phenomenon of drip-tips, there have been only three studies that have addressed the potential effect of drip-tips on epiphyll growth in any detail (Dean & Smith 1978, Ivey & De Silva 2001, Monge-Nájera & Blanco 1995). Monge-Nájera & Blanco (1995) studied artificial leaves with very short drip-tips, and thus their failure to find an effect on epiphyll growth does not mean such an effect is absent in leaves with more pronounced drip-tips. Also, they only measured bryophyte growth and neglected lichens. Dean & Smith (1978) found differences in epiphyll colonization between leaves with longer and shorter drip-tips, but these presumably grew under different light conditions, which could easily explain such differences (Lücking 1998a, 1999). The recent study by Ivey & De Silva (2001), which manipulated leaves by cutting off the drip-tips, is the most convincing in terms of an experimental approach to this question. However, the observation period covered only 9 d, while epiphyll communities develop over a period of several months to years (Lücking & Bernecker-Lücking 2002, Monge-Nájera & Blanco 1995, Sanders 2001, 2002; Sanders & Lücking 2002). In addition, the leaves were manipulated at an age of several weeks to months, after initial colonization by fungal and lichen diaspores, and it is the initial colonization, not subsequent thallus growth, that is most likely to be affected by the drainage of the leaf surface (Lücking 1998a).

The problem in looking for a correlation between drip-tips and epiphyll growth lies in the fact that in natural environments, the drip-tip factor cannot be separated from other variables to meaningfully test for its potential effects. The presence of drip-tips is usually a species-specific feature, although their individual sizes vary slightly depending on environmental conditions. Therefore, comparing leaves with and without drip-tips

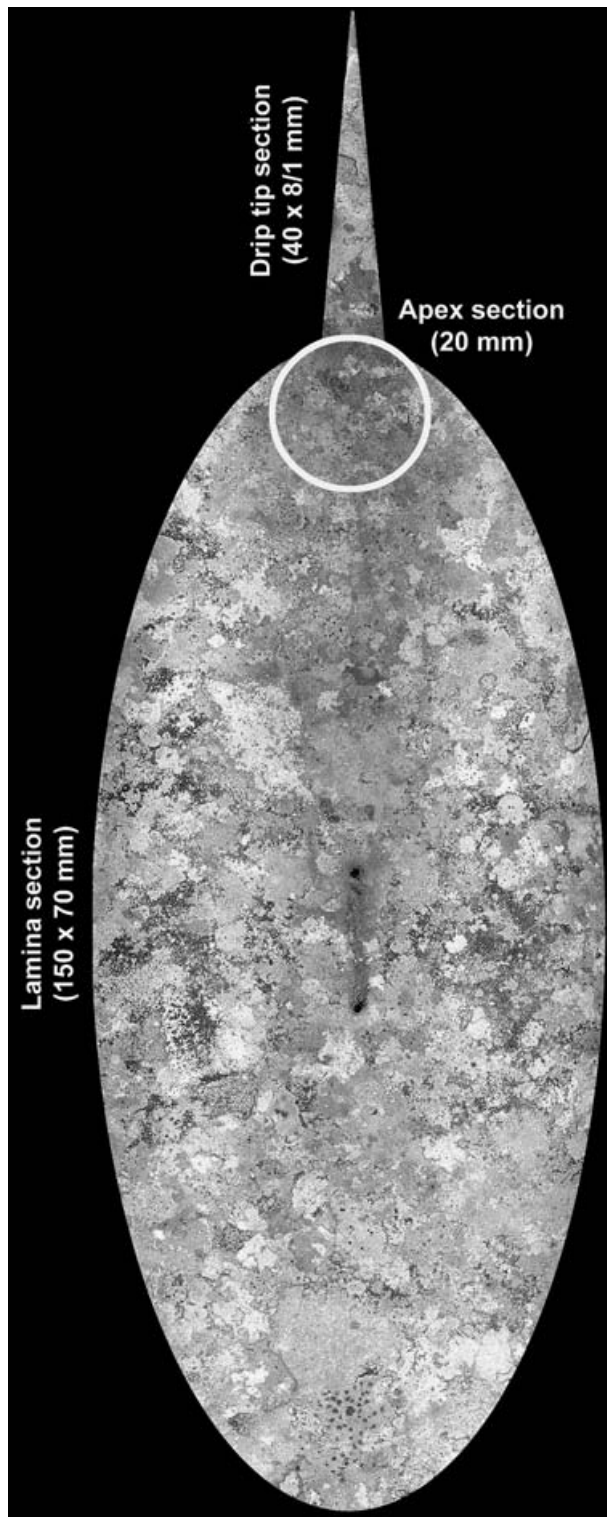
between different plant species and across microhabitats may yield misleading results. To circumvent these problems, one can take advantage of the fact that epiphylls colonize artificial substrata with smooth surfaces, such as plastic or glass (Lücking 1998b, Lücking & Bernecker-Lücking 2002, Monge-Nájera & Blanco 1995, Sanders 2001, 2002; Sanders & Lücking 2002, Sipman 1994). Monge-Nájera & Blanco (1995) tested the influence of leaf shape on epiphyllous bryophyte cover, and plastic cover slips turned out to be suitable substrates to study the development of epiphyllous communities, including early stages of lichenization (Sanders 2001, 2002; Sanders & Lücking 2002). Lücking & Bernecker-Lücking (2002) used artificial leaves to investigate the effect of leaf dynamics and spatial distance on small-scale diversity patterns.

Here, we used artificial leaves of a uniform, ellipsoid shape, half of which were provided with drip-tips. The experiment was performed at La Selva Biological Station, Costa Rica (McDade *et al.* 1994), where the epiphyllous biota is well-studied in terms of its taxonomy and ecology (Bien 1982, Lücking 1999). La Selva is the site with the highest reported number of foliicolous lichen species, with nearly 300, out of 800 known worldwide (Lücking 2001b). Coincidentally, several previous studies on drip-tips were carried out at this location (Ivey & De Silva 2001, Williamson 1981, Williamson *et al.* 1983).

We focused on epiphyllous lichens for three reasons. Due to their thallus structure, lichens intercept and reflect more light than other epiphyll organisms, and are therefore the primary suspect when it comes to potentially reducing leaf photosynthesis. Also, pronounced drip-tips are most common in lowland and seasonal rain forests (Schneider *et al.* 2003, Vareschi 1980), where lichens are the dominant component of epiphyll communities (Lücking 2001a). Finally, lichens have been neglected in previous studies, either intentionally (Monge-Nájera & Blanco 1995) or because the study design focused on early successional stages of epiphyll communities, where fungi are more abundant (Ivey & De Silva 2001). This is also the first study on this subject that identifies epiphylls to species level, which allowed us to monitor species richness and composition as variables potentially affected by drip-tips, and to compare the communities that developed on the artificial leaves with those growing on natural leaves in the study area.

## MATERIAL AND METHODS

Leaves were produced from WERGA FISKARS® (Austria) green plastic no. 202009 and cut into an ellipsoid shape (150 × 70 mm) to represent the mesophyll leaf-type common in tropical rain forests (Vareschi 1980), in particular *Ocotea atirrensis* (Lauraceae), which is common at the study site and supports a high diversity



**Figure 1.** One of the artificial leaves harvested after 38 mo of exposure, almost completely covered with lichen thalli. Sections delimited for data capture and analysis are indicated.

of epiphyllous lichens (Lücking 1998a, 1999). Half of the leaves included a pronounced drip-tip 40 mm in length and 8 mm basal/1 mm apical width (Figure 1).



**Figure 2.** Artificial leaves with and without drip-tips mounted on racks in a clearing at La Selva Biological Station (Costa Rica).

In February 2000, a total of 40 artificial leaves were exposed at two different microsites (20 leaves each) in primary rain forest at La Selva Biological Station (Costa Rica): one in the shaded understory (2–5% diffuse site factor), and one in a large, permanent clearing (10–30% diffuse site factor; determined by means of hemispherical canopy photographs). The two microsites were selected to test for potentially different effects of drip-tips under direct rain and indirect rain splash. At each microsite, leaves were fixed with plastic-wrapped garden wire in groups of five to four adjacent, 100-cm-high racks, each alternating leaves with and without drip-tips at an angle of 5° to simulate the slightly pendent aspect of natural leaves (Figure 2).

To assess the effect of the drip-tip on water flow on the surface of the artificial leaves, leaves with and without drip-tips were wetted with rain water using a dispenser, and drops falling off the leaf tips were caught using a calibrated test tube to measure their volume. Also, the time was measured that it took for the leaf lamina to dry out completely. The process was repeated for ten uncolonized leaves at the beginning of the study and for the same ten leaves with lichen cover after 38 mo.

After 38 mo of exposure, which corresponds to the time observed for epiphyllous lichen communities to reach a diversity maximum (Lücking 1998a, Lücking & Bernecker-Lücking 2002), the leaves were harvested in April 2003 (all but one drip-tip leaf from the shaded understory microsite were recovered). Each leaf was studied in the laboratory to quantify the development of epiphyllous lichen communities, and lichens were identified to species level using pertinent literature (see Lücking 1999) and reference collections housed at The Field Museum. In order to distinguish effects of drip-tips on different areas of the leaf, each leaf was divided into three sections: (1) the drip-tip (when present), (2) the apex, i.e. the distal area of the lamina (delimited by a 20-mm-diameter circle), and (3) the remainder of the lamina itself (Figure 1). For each section, three variables



were determined: (1) number of lichen species present; (2) total cover index (for the lamina section only); and (3) accumulation of debris. Cover index for each lichen species was determined by multiplying abundance and size indices, where abundance index was an estimate of the number of thalli present on the leaf (1–2 = 1, 3–5 = 2, more than 5 = 3) and their average size (0–3 mm = 1, 4–10 mm = 2, more than 10 mm = 3). Total cover index was calculated as sum of all individual indices. Accumulated debris was measured in four categories: absent = 0, 0–10% cover = 1, 10–30% cover = 2, 30–100% cover = 3.

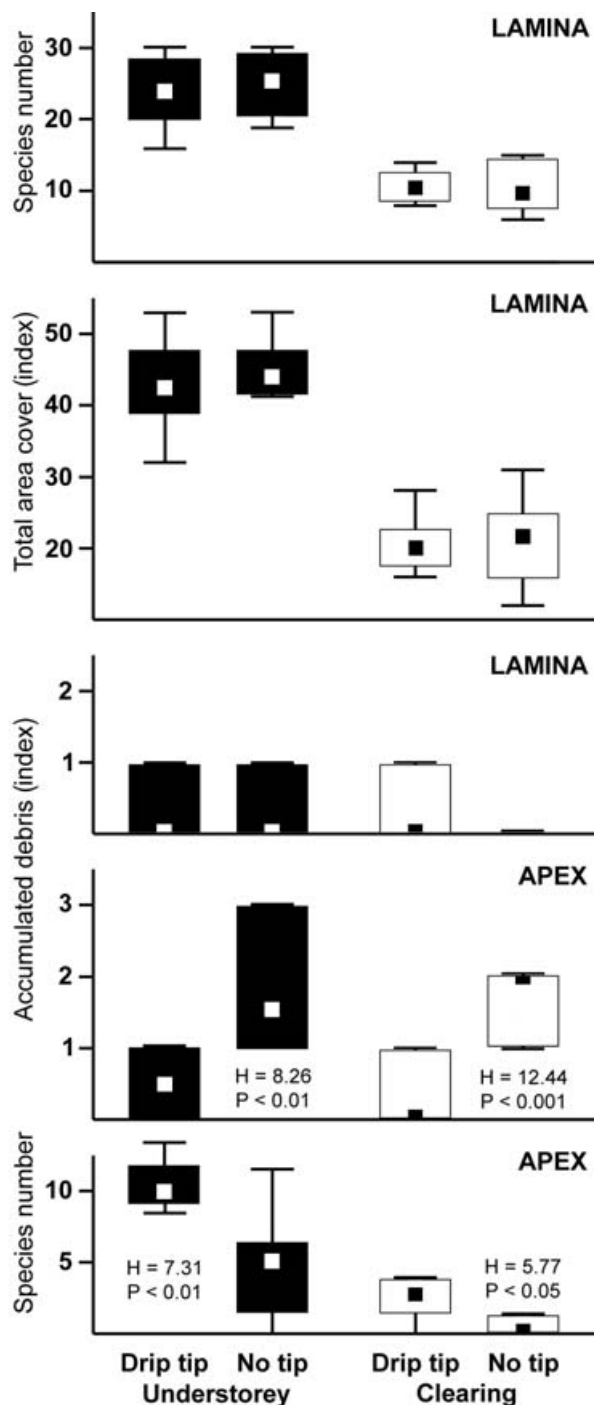
Cross-comparisons of variables among leaf-types were made using non-parametric Kruskal–Wallis ANOVA. Clustering of leaves was carried out by means of Ward's clustering algorithm using Euclidean distances of species cover indices. All analyses were performed in STATISTICA™ 5.0.

## RESULTS

A total of 93 lichen species was identified on the 39 leaves recovered, representing approximately one third of the foliicolous lichen biota known from La Selva Biological Station. Between 6 and 32 species were found on each leaf, including lamina, apex and drip-tip. The lichen communities were similar to those found in our previous study using the same type of artificial substrate, and to communities developing on natural leaves, as tested by cluster analysis (see Lücking & Bernecker-Lücking 2002).

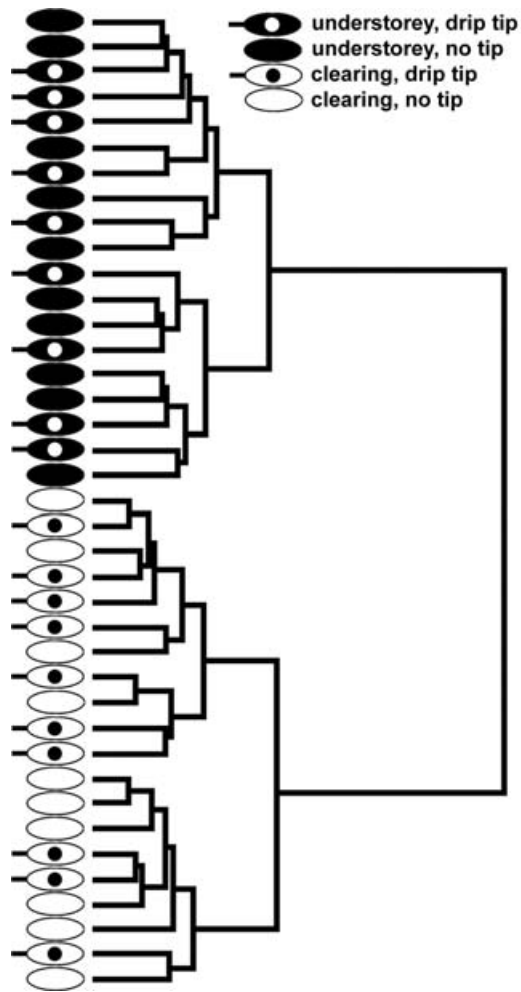
Water ran off artificial leaves with drip-tips constantly in small drops 8–30 mm<sup>3</sup> in size, and the surface dried within 15–30 min in the understorey and 7–15 min in the clearing. On leaves without drip-tips, while most of the lamina dried within the same time period, the water accumulated in the apical portion and either ran off in large drops 50–150 mm<sup>3</sup> in size or stayed there for a prolonged period until the water had partially evaporated. Leaves with lichen cover after 38 mo did not show significant differences in their drainage compared with those without lichen cover at the beginning of the study.

Average species number and total cover did differ significantly between leaves from the understorey and from the clearing, but there was no difference between leaves with and without drip-tips in the number of lichen species present on the lamina, nor in total cover (Figure 3). In the cluster dendrogram (Figure 4), leaves from the understorey and from the clearing formed two distinct groups with largely different species assemblages typical of each microhabitat: *Porina karnatakensis* was the dominant taxon on understorey leaves, while *Byssoloma subdiscordans* dominated on leaves from the clearing.



**Figure 3.** Box-and-whisker plots showing differences in lichen species number and total cover index, as well as accumulated debris (median, quartiles, min-max), on the leaf lamina and the leaf apex, between leaves with and without drip-tips, in the understorey and in the clearing. Significant differences found by Kruskal–Wallis ANOVA are indicated by the corresponding H and P values.

Yet, within each microhabitat, leaves with and without drip-tips were randomly distributed among groups and did not form distinct clusters, indicating that there was no



**Figure 4.** Cluster dendrogram of 39 artificial leaves with and without drip-tips, based on their lichen species composition. Leaves cluster according to their placement in the understorey and clearing, but not according to their leaf-type.

significant difference in lichen species composition related to drip-tips. Also, there was no significant difference in debris accumulated on the lamina across all experimental designs, that is microhabitats and drip-tips, although there was a tendency towards lower values on leaves from the clearing (Figure 3).

Significant differences, however, were found in accumulated debris, as well as in the number of lichen species present, in the apex section of the leaves (Figure 3): on leaves with drip-tips, less debris had accumulated in the apex section, while the number of species was higher.

## DISCUSSION

Our findings show that, although drip-tips affect the drainage of water from the leaf surface, they have no inhibitory effect on the establishment and growth of

epiphyllous lichens. On the contrary, the presence of more accumulated debris and fewer lichens in the apical portion of leaves without drip-tips suggests that drip-tips do, in fact, enhance epiphyll growth in this area, perhaps by flushing debris and effectively drying the surface of the apex section. This has already been suggested by Lücking (1998a), since the diaspores of many epiphylls can only adhere to the leaf surface if the water film present after rainfall is removed quickly. Also, in terms of the drip-tip effect, leaves exposed to direct rainfall under a clearing do not behave differently from leaves exposed to indirect rain splash in the understorey.

Because our study is the first to isolate the drip-tip factor from all other factors potentially influencing the establishment of epiphyll communities, and because we used a very pronounced drip-tip in our design, we present evidence that there is no correlation, either functional or evolutionary, between the formation of drip-tips and the development of epiphyllous lichen communities. We do not have data on other components of epiphylls, such as fungi, algae, and bryophytes. However, since lichens are the dominant component of epiphyll communities in lowland and seasonal rain forests (Lücking 2001a) and because their often white thalli are likely to affect light absorbance/reflectance of leaf surfaces more than other epiphylls, and since pronounced drip-tips are most common in these forest types (Schneider *et al.* 2003, Vareschi 1980), testing a potential correlation between drip-tips and establishment of epiphyllous lichen communities seems to be of primary interest.

So what is the function of drip-tips then? From the available evidence, including this study, there is little doubt that drip-tips do affect drainage of water from the leaf surface, but our observations suggest this effect to be limited to the leaf apex, while most of the leaf lamina seems to dry equally fast with or without drip-tips. Our studies confirm the results of Williamson and co-workers (Rebello & Williamson 1996, Williamson 1981, Williamson *et al.* 1983), that drip-tips primarily alter the size and frequency of water drops running off from leaves, although due to our experimental design with fixed plastic leaves, the volumes measured are higher than those found in other studies. According to the aforementioned studies, drip-tips might reduce splash soil erosion by decreasing the size and kinetic energy of secondary rain drops. This hypothesis is supported by the observation that drip-tips are more pronounced in the understorey than in the canopy (Richards 1996), because the difference in the kinetic energy between large and small rain drops decreases with increasing height, and hence there would be no evolutionary advantage for drip-tips above a certain height (Rebello & Williamson 1996, Williamson *et al.* 1983).

Since epiphylls are dispersed by rainwater and splash mechanisms (Lücking 2001a), it has also been suggested

that reduced splash energy would limit dispersal and establishment of potentially harmful organisms on leaf surfaces (Ivey & De Silva 2001). While this remains to be tested, the same study indicated that non-lichenized fungi behave differently from other epiphylls in establishing and growing more quickly, and that drip-tips differentially reduce the growth of fungi but not of other epiphylls. Other observations confirm that non-lichenized fungi do grow faster than other epiphylls (Sanders 2001, Sanders & Lücking 2002). However, because the drainage of the leaf surface affects initial colonization rather than growth, and both non-lichenized and lichenized fungi disperse primarily by ascospores and conidia, following the same adhesion mechanisms (Jones 1994, Lücking 2001a), there is little reason to assume that drip-tips would differentially affect their establishment. Also, since most parts of the leaf lamina do not seem to be affected by drip-tips, there would be little or no selective pressure to evolve such a feature if primarily related to fungal or other epiphyll growth. The same is true for the assumptions that drip-tips reduce passive leaching of substances from the leaf (Edmisten 1970), and that rapid drainage of the water decreases the reflectance of sunlight (Lightbody 1985). Because most of the lamina dries off quickly, whether there is a drip-tip or not, these effects would only occur within the small apical portion of the leaf.

Most certainly, the evolution of drip-tips cannot be attributed to a single function, but may be the product of pre-adaptations due to the particular ontogeny of budless leaves, interacting with multiple factors that contribute to a positive selection of a pronounced drip-tip in tropical rain forests. These factors might include splash soil erosion, photosynthetic performance, and leaching of substances, but this study demonstrates that there is no preventative effect on the establishment of epiphyllous lichen communities.

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